

THE CALYX IN *LYCIANTHES* AND SOME OTHER GENERA¹

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ABSTRACT

Vasculature and structure of calyces in *Lycianthes* and some related genera are analyzed to derive more generalized hypotheses on evolutionary trends in similar calyces. The generalized solanaceous calyx is seen as a whorl of five lobes enervated by five primary traces that branch in the lobes to form a pair of lateral veins and minor leaf-like venation. The adjacent laterals fuse basally to form an interconnector vein but are separate distally. There has been a tendency in these genera for the calyx lobes to fuse to higher levels, sometimes right to the top (perfect prefloration). There has been a tendency to fusion of lateral veins to higher levels, which gives rise to ten main traces or ribs in the fused area. The flower must egress from the bud and may do so in several ways. Where calyx prefloration is complete or nearly so, egress must involve stretching or tearing. Thus in *Lycianthes*, *Witheringia*, and *Capsicum*, the calyx becomes thin, with reduced, distorted venation under stretching stresses of floral egress in a region termed the sleeve. A tooth, here meaning any pointed structure accessory to a flower or inflorescence, is nearly ubiquitous in vascular plants, perhaps for protection. When the calyx teeth are completely fused, they no longer function as teeth. In some Solanaceae, this deficiency is remedied by enation of 'secondary' teeth below the sleeve. In *Lycianthes* they may be enervated by primary traces and fused laterals leading to the ten teeth in two series. These sequences of calyx evolution can be seen in some other families such as the Ericaceae.

In a group of genera in which the number of parts in a floral whorl is generally five, the frequent presence of ten teeth on the calyx of many *Lycianthes* species seems anomalous. These teeth are often in two alternating series and range in different species from small umbos to elongate, filiform processes many times the size of the calyx body. Closer examination discloses that these teeth are not apical on the calyx but appear from the side of the calyx below a ring or "sleeve" of tissue that terminates the calyx wall (Figs. 2-4, 7). Dunal (1852) grouped species like this into subsection *Lycianthes* of the genus *Solanum*, which was elevated to generic rank by Hassler (1917). The name *Lycianthes* was conserved over earlier names (McVaugh, 1973). Bitter (1919) and subsequent workers have expanded the genus to well over a hundred species. Placement of *Lycianthes* at the generic level was at first justified because of the reduced inflorescences and the presence of large stone cells in the fruit (Hassler, 1917; Bitter, 1914, 1919; Danert, 1969), yet the segregation of the group from *Solanum* has not met with the acceptance of all botanists. With a desire to understand the nature of the seemingly anomalous calyx structure and to reassess the validity of this genus, a study of calyx vasculature was undertaken. A considerable range

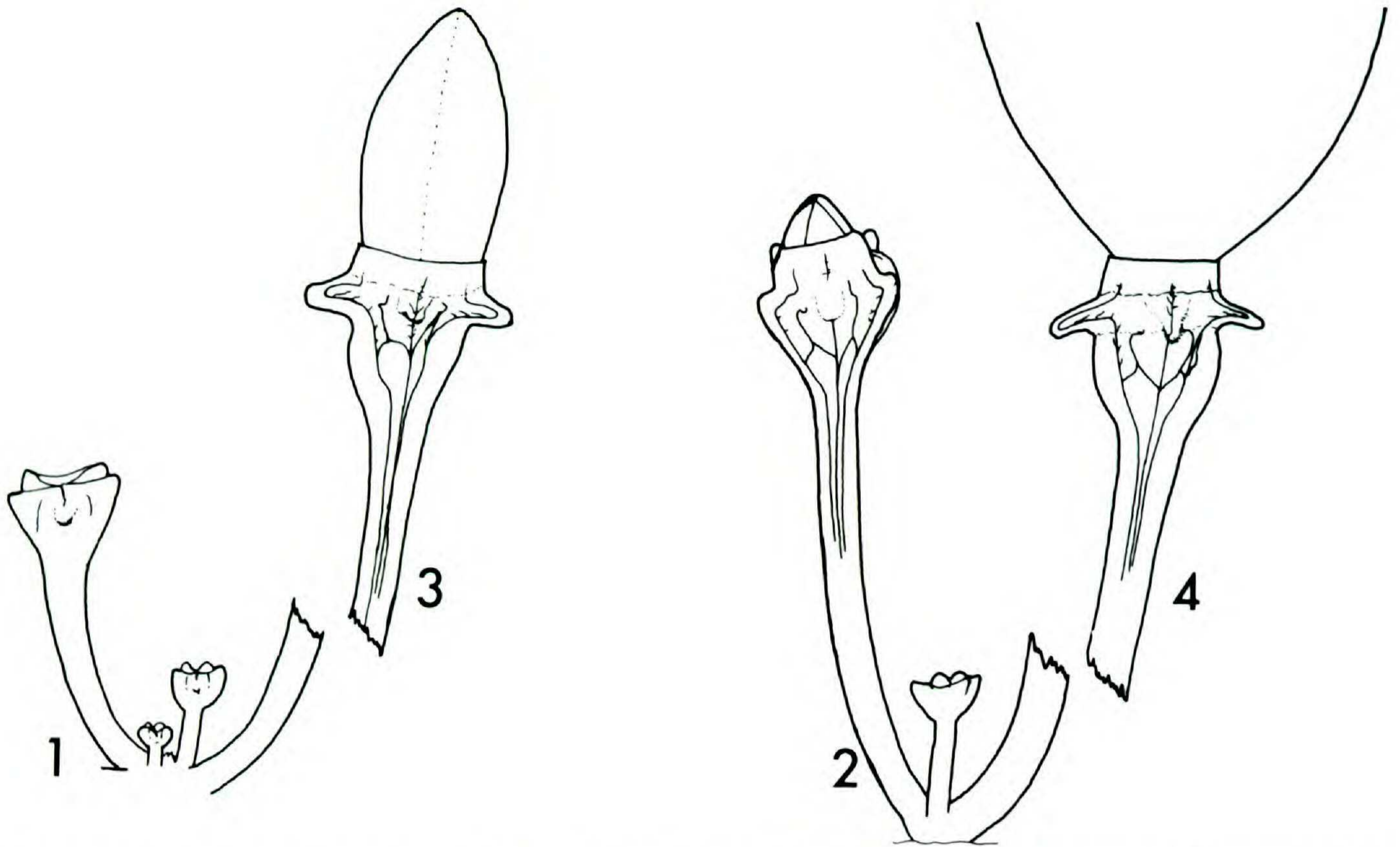
of material in related genera of Solanaceae, especially in subfamily Solanoideae, was studied, and material from other families was also examined. Some patterns in the evolution of calyces in the Solanaceae are apparent in other unrelated families.

METHODS

Traditional methods using sodium hydroxide and chloral hydrate were used to clear fresh, pickled, and dried flower buds and calyces of selected Solanaceae, and this treatment was sometimes followed by staining with safranin or basic fuchsin. These methods gave good three-dimensional views under a binocular dissecting microscope when material was held in vials in liquid but generally yielded poor photographic subjects. For photographs it was sometimes necessary to flatten the material on a glass slide and add a cover slip. Series of stained microscope sections of *Capsicum annuum* L., *Solanum seaforthianum* Andr., and *Oryctes nevadensis* S. Wats. were used for comparison. In addition, a great many flowers from many families were examined by naked eye and hand lens in the herbarium and in a living state.

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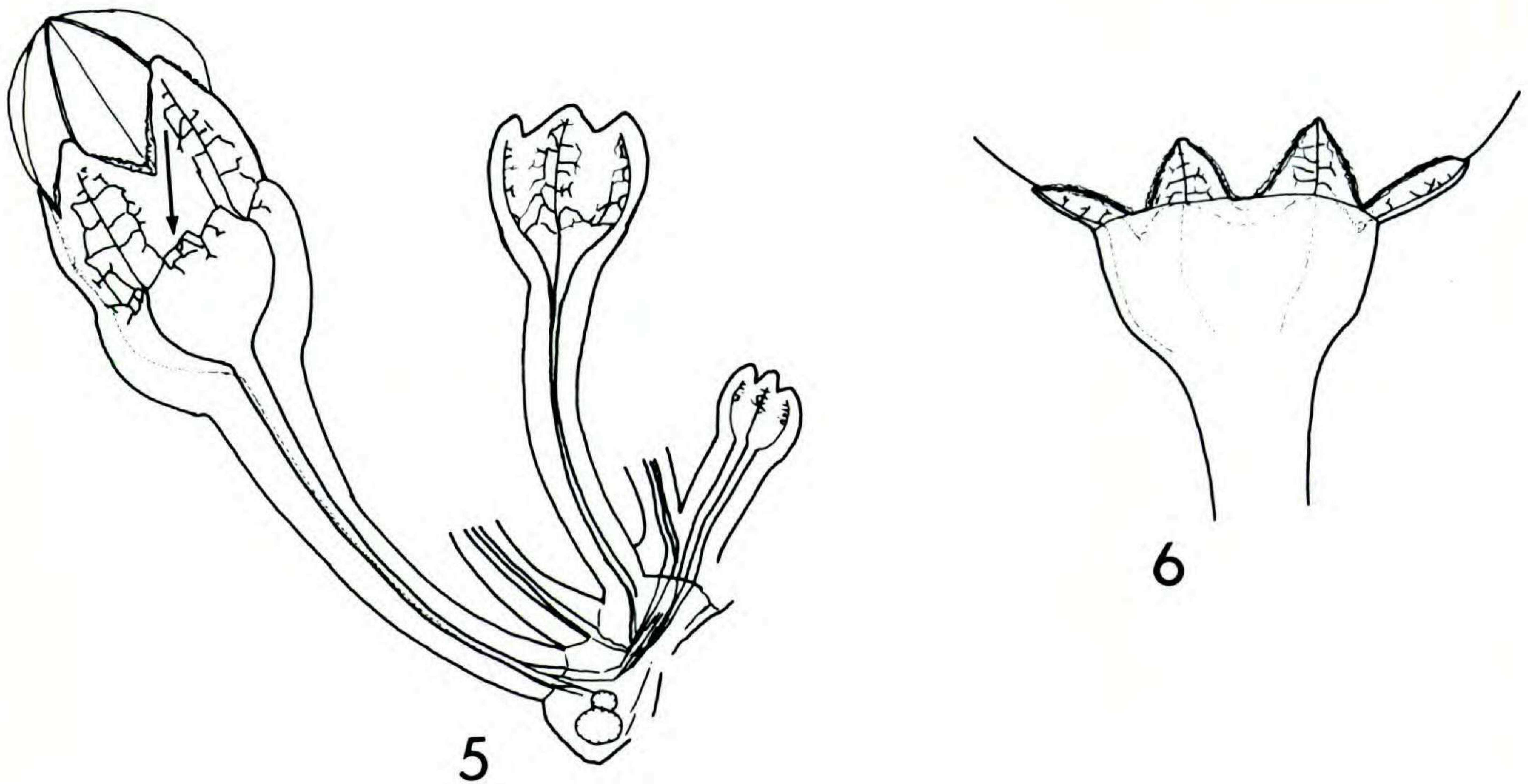


FIGURES 1-4. *Lycianthes maxonii* Standl. [After *D'Arcy 5507* (MO)].—1. Inflorescence with emerging buds. Calyx completely envelops the inner parts.—2. Corolla egresses from the calyx by stretching the apex into a thin sleeve. The teeth emerge beneath the sleeve area, and their vasculature moves out as they grow.—3. Corolla fully egressed and ready to open. The teeth have reached full size. The teeth enervated by the fused lateral veins are much smaller (see text).—4. Calyx in fruit showing intact sleeve and teeth.

THE GENERALIZED SOLANACEOUS CALYX

In many plant families, including the Solanaceae, the gamosepalous calyx consists of approximately five parts that are fused by their lateral margins to various levels, and the terms sepals and calyx lobes are often used interchangeably. Although the lobes may not in every case be homologous with the free sepals of the Archichlamidae, the studies of Copeland (1943) and Palser (1951, 1955) in the Ericaceae suggest that they are homologous in that family. In the Solanaceae examined in this study, the primary calyx vasculature consists of single traces running from the base of the pedicel to the tip of each lobe, differentiated even before the calyx lobes are evident as such. In cleared, stained whole material these traces maintain their identity throughout their length, although through the pedicel they are intimately associated and in serial sections they appear in this region as a siphonostele. Murray (1945) reported that in the Solanaceae gaps sometimes occur where the calyx traces leave the pedicel cylinder, but that this feature may vary even within a species. Techniques used in the present study did not distinguish parenchyma, and from the evidence seen of the vein architec-

ture the presence of gaps could not be ascertained. The veins leading into the petals and those leading into the sepals were recognizably distinct from one another throughout their length, even in the relatively constricted base of the pedicel, and they apparently continue independently from the base of the pedicel to the top of the flower (Fig. 5). Connections between the two perianth whorls through exchange of sepal and petal traces were not indicated by Murray and in this study were found only as rare exceptions. The nature of connections between this vasculature of calyx and corolla in *Solanum boldoense* Dun. is discussed below. In one other instance, in only one of several flowers of an ornamental pepper (*D'Arcy 7001*, MO), a vein was seen running between the calyx and corolla near the base of only one of the sepals. The single trace entering the calyx lobes in the Solanaceae is in contrast to reports (Carlquist, 1961) for many other groups in which the sepals are supplied by three or more traces arising from the stele or stelar plexus but is similar to some genera of Ericaceae (Copeland, 1943; Palser 1951, 1955), which are slightly more specialized than the most primitive members of the family.



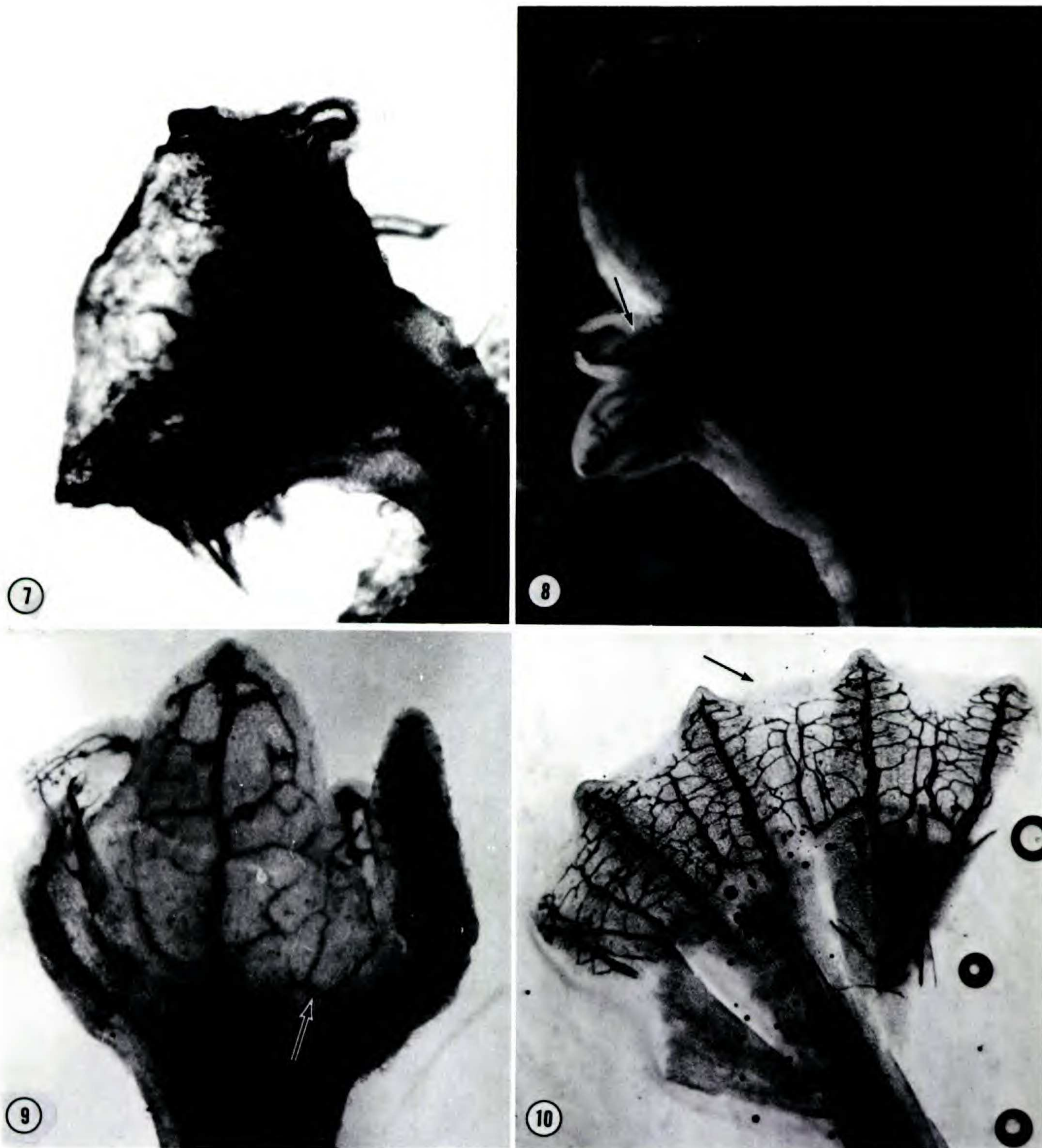
FIGURES 5, 6. *Solanum americanum* Mill. [After D'Arcy 15159 (MO)].—5. Developing buds. Primary traces develop leaf-like minor lateral venation. Note calyx lobes splitting at the sutures and absence of vasculature in the suture area. Interconnector vein is at arrow.—6. Fruiting calyx with lobes split to the base.

Almost as soon as the calyx lobes are evident in the bud, a system of minor venation appears in each lobe that is usually soon oriented into two lateral veins flanking the midvein and a vein linking the basal, tangential portions of the laterals to form a prominent 'interconnector' vein (Figs. 5, 9). The interconnector may later assume structural importance in the fruiting calyx, as in the physaloid genera (*Physalis*, *Nicandra*, *Withania*, etc.). Other minor venation resembles that of a foliage leaf presenting a more or less acropetal, pinnate configuration on each side of the midvein (Figs. 5, 9). In her serial sections, Murray viewed the interconnector as anastomoses of the sepal traces, which at a slightly higher level broke into usually three separate veins. In the Solanaceae the interconnector often does not appear as such until after the minor venation has taken on its main outline, hence it is seen as secondary in an ontogenetic and perhaps phylogenetic sense. The pattern of a single sepal trace expanding into an interconnector and three major veins can be observed in other families such as the Boraginaceae, Scrophulariaceae, and *Cerastium* in the Caryophyllaceae. In many species of Boraginaceae there are two interconnectors, one at the base of the calyx and the other nearer the top, seemingly formed from venation displaced from the intermediate region by tight compression of the calyx around hard fruits.

Fusion of adjacent calyx lobes may involve ground tissue alone or both ground tissue and

vasculature, and the level and nature of fusion may be usually of generic significance. Only one study is known that documents the developmental nature of calyx fusion in the Solanaceae. The fusion of ground tissue was investigated in *Datura* by Satina (1944), who used chimeras of different ploidy levels to show that in that genus the fusion of ground tissue is ontogenetic. The fusion takes place at a very early stage, and stages where fusion has not yet taken place cannot be identified by macroscopic methods. In many other genera of Solanaceae, from the time the flower bud is 1–3 mm long, there is little or no further alteration in length of the free sepal tips. From this it is assumed that by this stage the process of fusion is complete, but there is often a subsequent enlargement of the region of fusion.

After fusion of adjacent sepal margins, fusion of adjacent lateral sepal veins may take place, and the fusion is usually for most of the length of the longitudinal portions of the veins producing a second series of longitudinal veins alternate with the primary traces (Figs. 2, 4, 10). Such fusion is always the case in *Lycianthes* but appears only with irregularity in *Capsicum* (Fig. 10), often varying from sepal to sepal and from flower to flower. Fused laterals were put to taxonomic use by Waterfall (1958, 1967), Rydberg (1896), and others in the genus *Physalis*, in which groups of species were distinguished as being five-angled, 10-angled, or round, the condition mainly consequent on the state of fusion and development

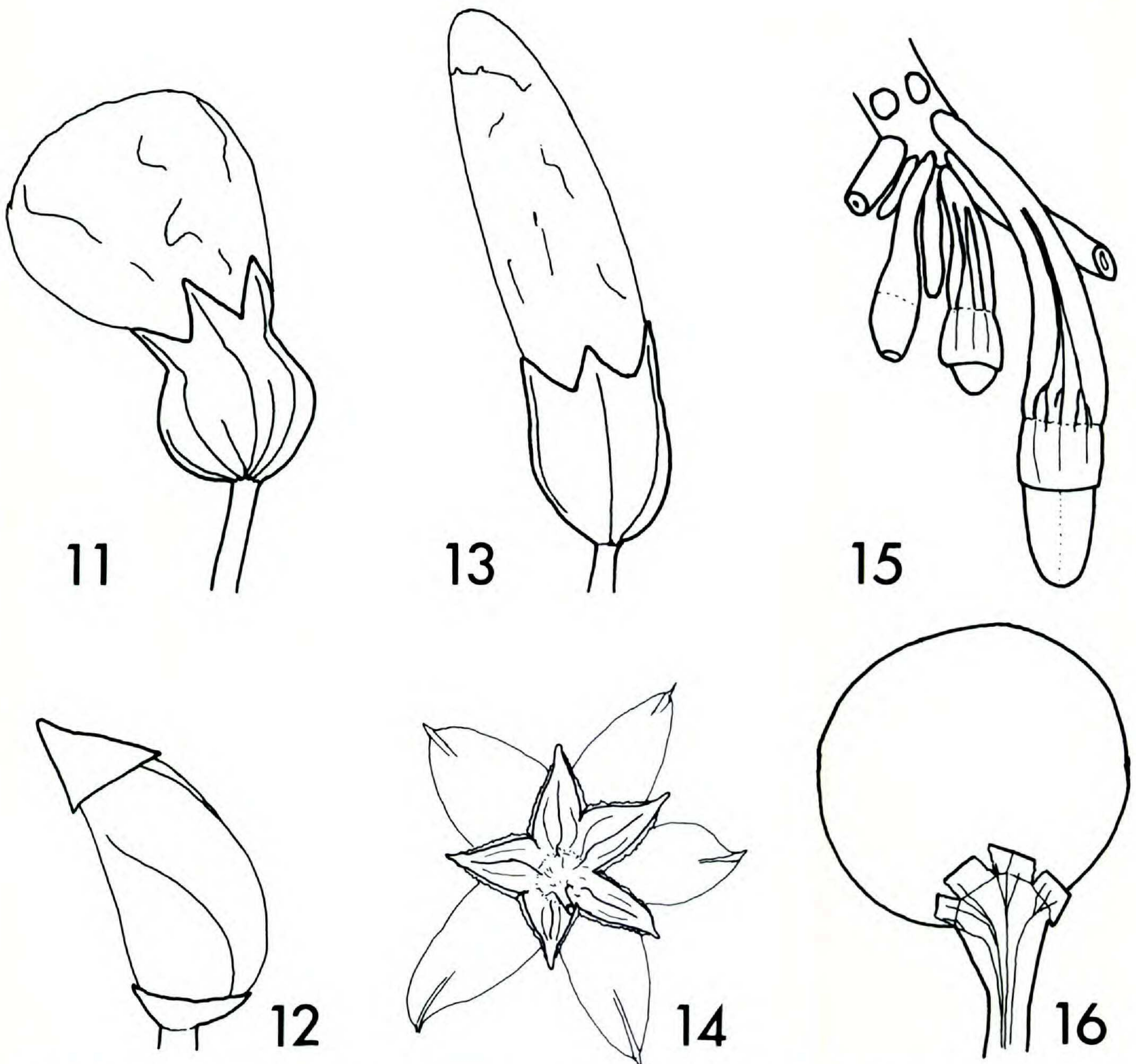


FIGURES 7-10. 7. Calyx of *Lycianthes maxonii* Standl. showing the reduced vasculature in the sleeve and the primary traces which have bent out within the teeth. — 8. Calyx of *Lycianthes guianensis* (Dun.) Bitt. showing how the primary traces bend out within the teeth and the minor venation is directed basepetally as a result of this repositioning (arrow). — 9. Calyx of *Solanum americanum* Mill. showing how the minor venation arising from the primary trace resembles the venation of a leaf. The interconnector can be seen at the arrow. — 10. Calyx of *Capsicum annum* L. opened to show the vasculature. The rudimentary sleeve can be seen at the apex between the reduced teeth (arrow). In this calyx the laterals have fused. It is speculated that the main teeth here are actually secondary teeth derived by outbending below the sleeve that have refused back against the primary traces (see text).

of the sepal laterals. Such fusion of apparently homologous laterals is common, and was observed to occur in the Phrymaceae, in nearly all Lythraceae and Labiatae, common in the Caryophyllaceae (for example, *Cerastium*), but uncommon in the Scrophulariaceae.

FLORAL EGRESS IN THE SOLANACEAE AND IN GENERAL

For the expansion of flowers in many families the corolla and often the stamens and stigma must find their way out of the enclosing outer



FIGURES 11-16. Modes by which floral egress from the calyx is achieved (examples).—11. Prefloral Egress: the flower egresses early and undergoes development and expansion outside the calyx (? *Margaranthus*).—12. Calyptrate Egress: the top of the calyx separates to leave the flower free to expand (*Magnolia*).—13. Distensive Egress: here the calyx stretches slightly to permit egress, but there is no marked distortion (*Anaemopaegma*).—14. Dehiscent Egress: in *Solanum*, only the tips of the calyx lobes are free in bud, but bigger lobes result from splitting at the sutures.—15. Distensive Egress: egress is by stretching of the distal portion of the calyx and a marked sleeve is produced (*Witheringia*).—16. Dehiscent Egress: *Witheringia* has distensive floral egress, but there is dehiscence for egress of the fruit.

perianth, which is usually the calyx. The mode of egress can be seen by observing the expansion of flowers in living material and often by observing dried herbarium specimens. In the flower with free sepals, egress of the corolla and other floral parts from the calyx is readily effected by outward movement of the sepals, but where there is fusion of the sepals, other arrangements may be necessary to permit egress of the pistil as it develops at anthesis and into fruit (Figs. 11-16). Where fusion of the calyx involves only the basal portion of the sepals, egress may involve no more

than a slight stretching of the calyx without significant alteration of shape (Fig. 13). This is the case in many species of Verbenaceae (for example, *Clerodendrum splendens*), Polemoniaceae, Plantaginaceae, and other families, but in most Solanaceae there is high enough fusion that other mechanisms are invoked. Where fusion has progressed to unite upper portions of the sepals, egress may require either stretching and major distortion or tearing of the calyx at some point. In *Solanum* and *Lycopersicon* the sepals are usually fused except for their tips, and the sutures

or regions of fusion between them tear open in a valvate fashion to permit egress (Fig. 14). This is also found in *Symphytum* (Boraginaceae). The tearing may begin before the tip of the budding corolla reaches the length of the sepal tips or may be delayed until the corolla actually begins to unfold. Further tearing may take place with expansion of the fruit (Figs. 6, 16). In *Solanum*, *Lycopersicon*, and many other solanaceous genera, in which floral egress involves tearing at the sutures, there is no vasculature in the region of tearing. Where the calyx is fused to the top of the sepal tips as in *Lycianthes*, *Witheringia*, and *Anaemopaegma* and in many other Bignoniaceae, instead of by splitting, floral egress is achieved by stretching of the upper portion of the calyx (Fig. 13, 15). The stretched top portion of this calyx is manifestly thinner and smoother than the lower unstretched portion, and its appearance suggests that important stresses have been present as egress was effected. This area is the "sleeve" referred to above in the introductory description of the *Lycianthes* calyx. Not only is the surface sharply demarcated but the vasculature is much reduced or even absent in the stretched area. Where floral egress is by major stretching of this sort, possibilities for egress by splitting along the sutures of the calyx would be lessened by the presence of vasculature derived from lateral veins in the region between the primary calyx traces. Where sepals are fused to the top of the calyx leaving no opening, the calyx prefloration is termed complete. Here at least some tearing is necessary to create a circumference that can be stretched or to provide, by the tearing itself, a large enough opening for the floral parts to expand. Possibilities for splitting along the sutures is lessened by the presence of vasculature in this area; in genera such as *Solanum* and *Lycopersicon* in which egress is by splitting along the sutures, there is no vasculature or fusion of lateral veins in the suture area. Where there is fusion of laterals and hence vasculature in the suture areas, the tearing may continue down the calyx wall without regard to the position of vasculature. This sort of splitting without regard to the vasculature is a common situation, occurring in many genera with more advanced calyces: *Brugmansia*, *Bourreria pulchra* (Boraginaceae), *Silene* (Caryophyllaceae), *Tabebuia* (Bignoniaceae), etc. Where floral egress is by stretching, irregular splitting for egress of the fruit may also occur as in some species of *Witheringia* (Fig. 16). A special case of splitting without re-



FIGURE 17. Stylized drawing of *Lycianthes* showing vasculature running into the teeth and then back to disappear in the sleeve.

gard to the vasculature is the circumscissile or calyptrate dehiscence of the calyx in *Datura* and in *Eschscholzia* (Papaveraceae) and *Lundia* (Bignoniaceae). Species of *Margaranthus* (Fig. 11) and of *Salvia* (Labiatae) appear to undergo a prefloral egress in which the floral parts egress at an early stage and undergo much of their development outside the confines of the calyx. The above listed modes of floral egress are not exclusive categories, and variations occur that combine two or more of these methods. Thus in some species of *Cyphomandra* and in *Cordia polycephala* (Boraginaceae) prefloration of the calyx is complete except for a minute apical pore that may be stretched or split or both. In some species of *Magnolia* (Magnoliaceae) floral egress (from enclosing bracts instead of a true outer perianth) is achieved by calyptrate or longitudinal dehiscence or sometimes by both on the same flower (Fig. 12). Egress may not be necessary in some cleistogamous flowers, and in *Aristolochia* (Aristolochiaceae) the outer perianth expands into a corolloid structure with the androecium and gynoecium well enclosed during flowering. Mechanisms for egress of fruit are often related to systems of fruit dispersal. In the phys-

aloid genera and in species of *Abutilon* (Malvaceae) and *Saccellium* (Boraginaceae), etc. the bladderly calyx may be a means of adapting a berry or achene-like fruit to wind dispersal. There are various stages from loosely investing calyces, as in *Physalis*, to tightly fitting calyces, as in *Trapa* and *Globularia* (stone fruits), *Solanum rostratum* (dry berry), and *Cordia sebestena* of the Boraginaceae (stone fruits). In the two last mentioned cases floral egress is by splitting and stretching, but the portal so formed does not enlarge, and the calyx and ovary are in snug contact for much of their development. Such a situation might logically precede fusion of juxtaposed parts for the evolution of the inferior ovary in groups such as the Rubiaceae, Ericaceae, and Cucurbitaceae where the tissue surrounding the ovary is considered to be appendicular. "If epigyny in the Rubiaceae has a perigynous ancestry, there is no indication of it in the species alive today" (Cronquist, 1970), but if evolution proceeded from an enveloping calyx as suggested above, there was probably no need for perigyny as an intermediate stage. Although an inferior ovary usually avoids the need for egress of fruit, a variety of modes of floral egress can be seen in families with epigyny.

THE WIDESPREAD OCCURRENCE OF TEETH

The calyx is often an enveloping structure made up of several pointed elements. These pointed elements can be viewed as teeth, a term used here for pointed structures accessory to a flower or inflorescence without regard to homology or derivation. It is necessary to emphasize the very widespread presence of such pointed structures in the architecture of inflorescences. In dicotyledons and monocotyledons alike the floral parts are regularly provided with a calyx terminating in one or more pointed elements, and where this is lacking an analogous form is often taken by pointed bracts or an awn. Such diverse groups as *Taxus*, *Ephedra*, *Najas*, *Saururus*, *Mirabilis*, and *Taraxacum* that lack toothed calyces have approximately similar structures derived from bracts. Teeth accompanying fertile parts are widespread and hence would seem to have important utility or selective value.

THE PROVISION OF TEETH IN LYCIANTHES

Where fusion has proceeded along the entire length of the sepals and calyx prefloration is com-

plete, the flower bud is no longer provided with teeth. Not surprisingly, some species that have lost their functional teeth in this way have evolved teeth that are not homologous with the teeth of an incompletely fused calyx. In species of *Lycianthes*, *Capsicum*, and *Witheringia* these non-homologous or secondary teeth are produced around the side of the calyx and are often vascularized by outbending of the calyx venation at the points where they occur. Evidence of the nature of these secondary teeth is clear in the pattern of vasculature in many species. The primary calyx traces may arch outwards into the secondary teeth and return again to the calyx wall to end in the terminal or sleeve portion of the calyx. (Figs. 1-4, 7, 8, 17). In *Lycianthes* (Figs. 8, 17) the pinnate minor venation is consequently now directed downwards with respect to the form of the teeth but is still acropetal with respect to the traces it flanks and to the calyx as a whole. In different species, these secondary structures range from small lumps or umbos to elongate filiform teeth in some *Lycianthes* groups and to substantial acute teeth in *Capsicum chacoense*. In *Lycianthes* where the lateral sepal veins are fused to form a second series of vertically oriented veins, there is often a second series of secondary teeth vascularized by an outbending of the bases of the fused lateral veins. In some species of *Lycianthes*, *Capsicum*, or *Witheringia* in which outbending of the primary traces is slight, secondary teeth or umbos may not occur with regularity at each primary trace. Calyces of *Lycianthes rantonnei* may have from zero to ten teeth on different flowers on the same plant. Where the secondary teeth are small, they often shrink on drying and may be missed in casual viewing of herbarium material. Besides the solanaceous cases discussed here, what may be secondary teeth occur in at least a few other flowering plant groups such as *Lagerstroemia indica* (Lythraceae), *Hamelia* (Rubiaceae), and *Amphilophium* (Bignoniaceae).

CALYX PATTERNS IN SOME RELATED GENERA

Cyphomandra. Adjacent laterals are not fused and sepals are fused to or near to the top of the calyx. Floral egress is by a combination of splitting and stretching.

Brachistus. The sepal tips are not fused and floral egress is achieved by small amounts of tearing and stretching. There are no evident swellings or ridges on the calyx wall, and there is no sleeve. It was partly on the basis of this primitive calyx

that D'Arcy et al. (1981) separated *Brachistus* from *Witheringia* and restricted it to three species.

Capsicum. In *Capsicum annuum* the minute sepal tips are free and floral egress is effected with minor stretching. Adjacent sepal laterals are usually close but usually not fused. The base of the calyx may develop a slight swelling and out-bending of the vasculature from its otherwise cylindrical structure. *Capsicum chinense* has a conspicuous but unvascularized swelling or ferrule where the pedicel flares into the receptacle or calyx base. *Capsicum chacoense* and *C. baccatum* have well-developed secondary teeth, which appear externally like ordinary free sepal tips, but clearing of the tissue reveals that these teeth are secondary, and the primary vasculature runs first to the tip of the teeth and then back down to the calyx and into the sleeve. The basipetal minor venation seen in the teeth of species of *Lycianthes* was not seen in *Capsicum chacoense*. The sleeve in *Capsicum* is inconspicuous.

Jaltomata. The bud of *J. procumbens* is a flat-topped cylinder. The calyx lobes are coherent for their full length, there are no discernible free tips, and prefloration is apparently complete. The lateral sepal veins are fused as far as the rim of the flat bud, while along both the primary sepal traces and the fused laterals, ridges run from the base of the receptacle to the rim of the bud. These ridges are suggestive of incipient teeth or umbos in the manner of the secondary teeth of *Lycianthes*.

Lycianthes. Adjacent laterals are always fused and floral egress is effected by stretching of the calyx rim, which produces a recognizable sleeve. There is a tendency for the development of secondary teeth from the side or base of the calyx wall and for these to be vascularized by out-bending of the primary sepal traces and the longitudinal portions of the fused laterals.

Lycopersicon. Calyces are like those in *Solanum*, but the free sepal tips are proportionately longer.

Margaranthus. The calyx is like that in *Physalis* but splitting is very short. Much of floral development seems to take place after egress has been initiated, and this prefloral egress can be used for routine separation of the similar *Physalis lobata* Nutt.

Nicandra. Prefloration is complete and floral egress is effected by splitting at the sutures. The interconnector becomes lignified in the accres-

cent calyx. Two well-spaced laterals appear on each side of the sepal midvein.

Physalis. Prefloration is like that in *Solanum*, and floral egress is by longitudinal splitting at the sutures. Adjacent laterals are mostly fused, but in some species there are two pairs of laterals as in *Nicandra*. The interconnector usually becomes lignified in the accrescent fruiting stage.

Solanum. Adjacent calyx teeth are fused partway up, but there is no fusion of lateral veins except for the interconnector. Floral egress is by splitting at the unvascularized sutures. In some cases there is further splitting in fruit. Exceptions are discussed below.

Witheringia. There is no fusion of adjacent laterals, and floral egress is achieved by stretching, often producing a distinct sleeve. In some species there are umbos at the base of the calyx, and in fruit these species may be difficult to distinguish from species of *Lycianthes*. Some species split for egress of fruit. This calyx appears to be highly evolved in contrast to the primitive calyx in *Brachistus*.

SOME SPECIALIZED EXCEPTIONS IN SOLANUM

In *Solanum seaforthianum* floral egress combines some splitting with stretching, and there are no other apparent deviations from the normal pattern. But in the closely related *S. boldoense* of Cuba (Fig. 19) the base of the calyx is expanded into a conspicuous cupule or ferrule, and there is a reticulum of fine venation extending below the connector, which appears to be supplied by traces from both the corolla and the calyx. *Solanum surinamense* Steud. (Fig. 8) has a fine reticulum like the two species just mentioned and five prominent apical unvascularized lobes. These three exceptions have floral egress by stretching. Other species with prominent basal cupules, *S. hazenii* and *S. antillarum*, have no departures from the normal *Solanum* calyx vasculature.

LYCIANTHES AS A GENUS

A distinctive feature of plants assigned to *Lycianthes* is the structure of the calyx. This calyx is quite different from the calyx of *Solanum* and is more like that of species of *Capsicum* and *Witheringia*. Although a few species of *Solanum* seem to approach *Lycianthes* in the manner of portal opening, they are not good candidates for consideration as intermediates between *Solanum* and *Lycianthes*. The calyx in *Solanum* with

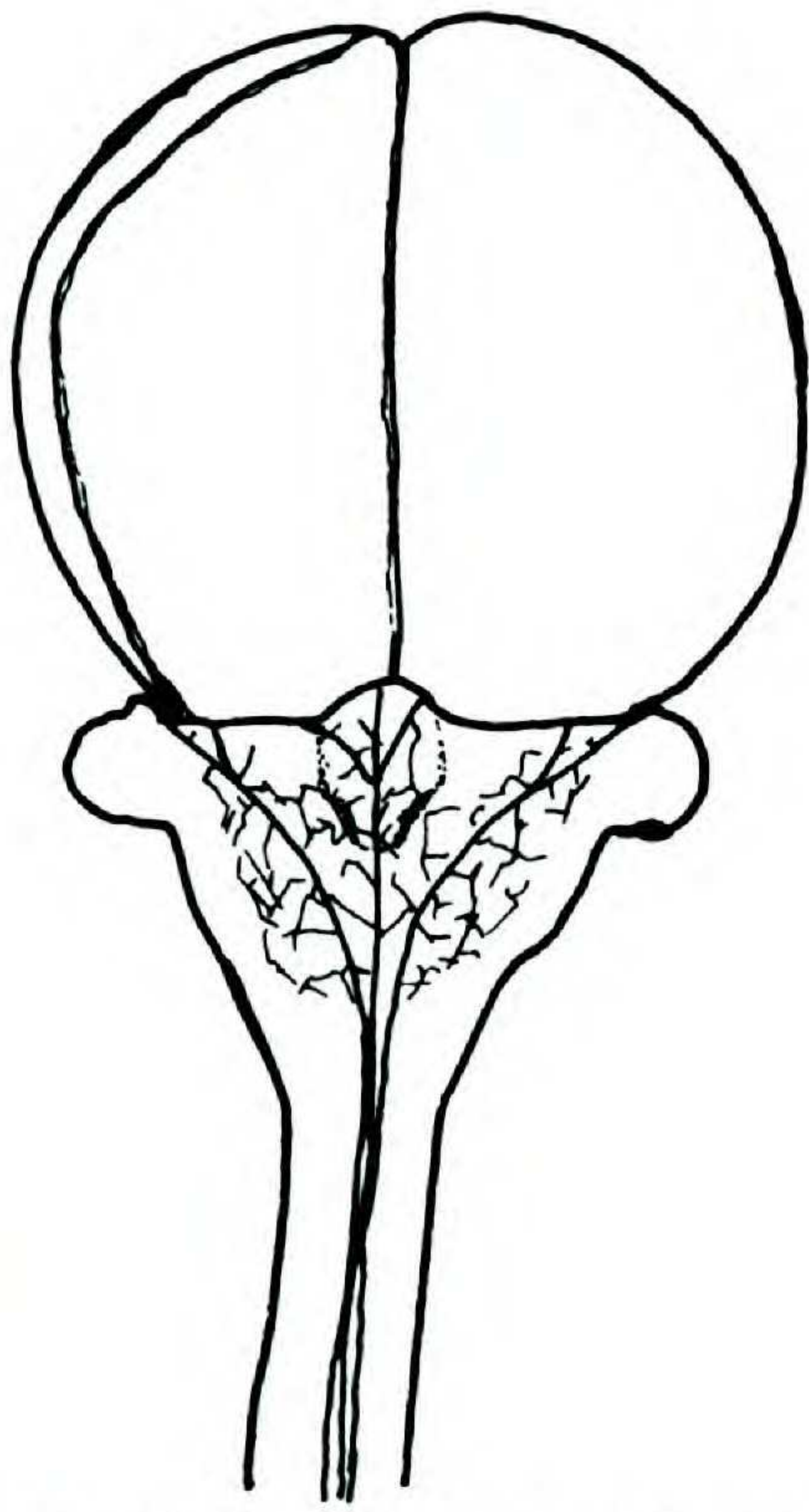


FIGURE 18. The exceptional calyx vasculature of *Solanum surinamense* Steud. Note the proliferation of minor venation below the unvascularized teeth.

its less complicated vasculature should probably be considered primitive among the genera listed above and that of *Lycianthes* to be much more advanced.

Other characters separating *Lycianthes* are generally inconclusive. Chromosomes, wood histology, and pollen have provided little assistance. The stone cells invoked by Bitter (1919) occur in other genera and also in *Solanum*. Reduced inflorescences, entire leaves, and spinelessness are useful but are not generic characters. Perhaps improved chemical information will provide better demarcation. There may nevertheless be some important biological differences: there are few specimens in herbaria (Nee, 1981; Symon, 1986) and many of the species flower nocturnally (Nee, 1981).

Although clearly distinguished only by its calyx, this character indicates a significant advance in the evolution of at least one floral organ over the less specialized genus *Solanum*. From a practical point of view, it is useful to consider the more than one hundred species of this advanced group as a generic entity with its own name. This is helpful in gaining accessibility to the literature and to specimens filed in herbaria. Species of this group are with few exceptions easily identifiable by a glance at the calyx, and confusion in dealing with these exceptions generally relates to their similarity to *Witheringia* or *Capsicum* and not

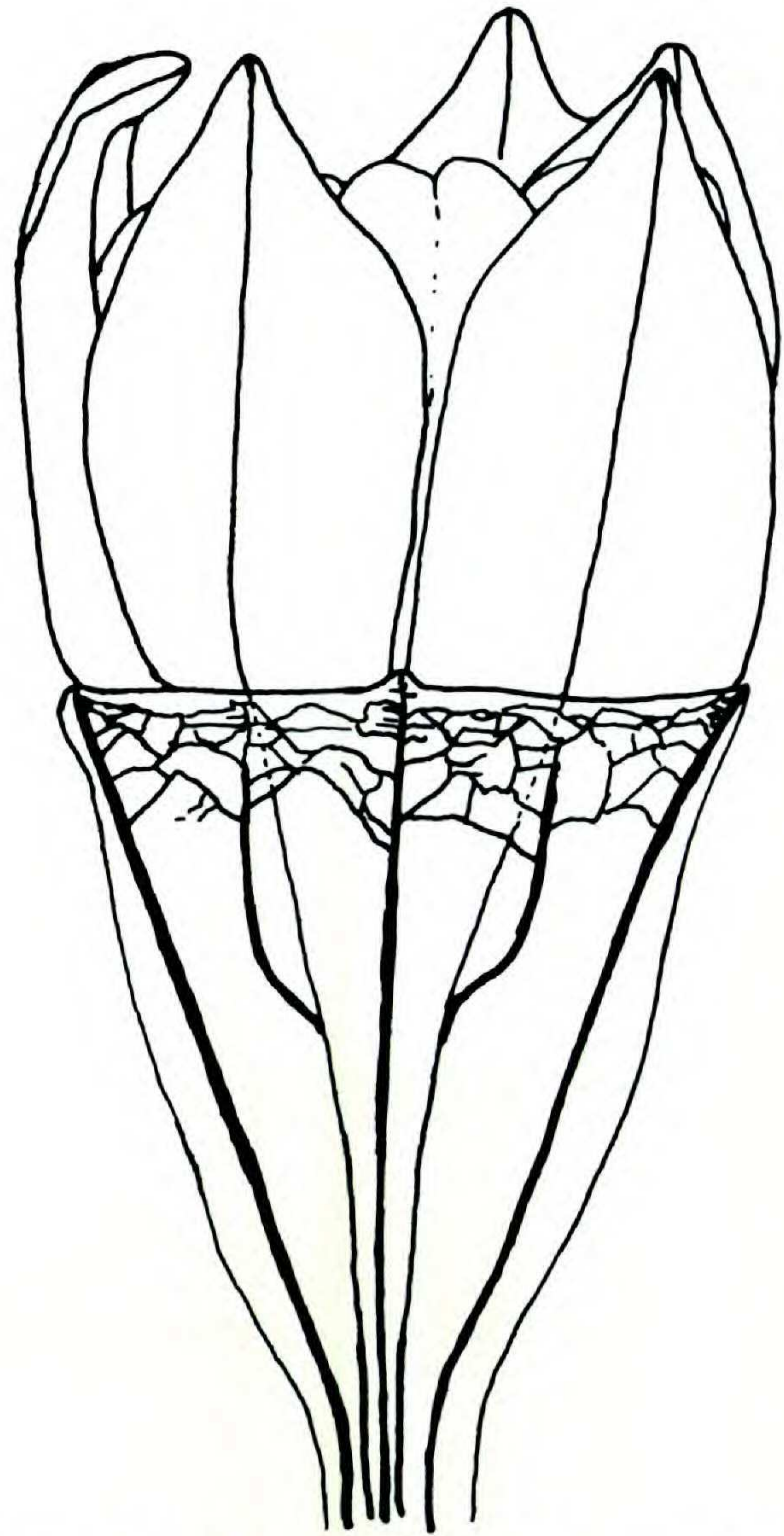


FIGURE 19. The exceptional calyx vasculature of *Solanum boldoense*. Note connection between calyx and corolla traces.

to *Solanum*. The diagnostic presence of a sleeve and the frequent presence of ten lateral teeth in two series distinguish it readily from *Solanum*.

THE CALYX IN PHYLOGENY AND TAXONOMY

Studies in the Lauraceae (Kasaplilg, 1951), Ranunculaceae (Tepfer, 1953), and other primitive families, usually with distinct sepals, generally show that the sepals are vascularized by a series of traces oriented in much the same way as the traces in leaves of the same plant (see Esau, 1960, 1965). The work of Copeland (1943) and Palser (1951, 1955) in the Ericales lends support to the view that the calyx lobes in the Sympetalae are homologous with those of the more primitive families. Their work outlines a sequence of calyx evolution that parallels the trends in specialization of other organs in those plants. The sequence of evolution of primary calyx vasculature in the

Ericales may be summarized as follows (sepals are usually five):

1. Three independent traces per sepal (15 gaps) (*Befaria*, *Leucothoe racemosa*, etc.).
2. Three traces per sepal (ten gaps): median plus laterals derived from an intermediate sepallary trace common to two sepals (*Chamaedaphne*).
- 3a. One trace per sepal that soon divides into a median and two laterals (five gaps) (*Elliottia*, *Gaultheria*, *Ledum*, etc.).
- 3b. Three traces per sepal (five gaps): median plus laterals derived from intermediate petal bundles (*Kalmia*, *Pyrola*, *Clethra*, etc.).
4. One trace per sepal (five gaps): no laterals (*Cassiope mertensiana*).

In the Ericales these branching patterns occur in the receptacles, and at the level of sepal expansion the laterals may branch into five to nine veins. From stage 2, there is the possibility of advancement to either stage 3a or 3b.

In the genera of Solanaceae here examined, the primary calyx vasculature is all at stage 3a, but at higher levels in the calyx, the vasculature shows two developments not seen in the Ericales: fusion of sepal laterals and enervation of secondary teeth or appendages. Fusion of calyx parts has opened new possibilities for evolution of vasculature. The degrees of calyx fusion and possibilities for egress are categorized in Table 1.

ADVANCES AND REVERSALS OF CALYX EVOLUTION

One may envision a sequence of evolutionary steps that would yield a condition so like the starting point that the advancement that had occurred in between would not be detected. Such a sequence may have taken place in *Capsicum*. It is probable that the calyx of *Capsicum chacoense* evolved from a primitive stage such as one sees in *Solanum* to its present form by a sequence like that in *Lycianthes*. If the secondary teeth were not of selective value under new environmental conditions they might become fused back into the calyx wall and sleeve. And if the sleeve was not of selective value it might disappear. Then there would be a rudimentary sleeve, and the formerly outbent vasculature of the secondary teeth would be juxtaposed radially against the primary trace and would tend to fuse with it. There would remain a rudimentary sleeve and probably small teeth, which would be the

TABLE 1. Degrees of calyx fusion and possibilities for egress.

Perianth Structure	Level of Advancement	Mode of Egress
Outer perianth wanting	1.	No confinement
Outer perianth of free segments (sepals)	1.	No confinement
Outer perianth fused to near the base	2.	Expansion
Outer perianth mostly fused, tips free	3.	Stretching
Outer perianth fused to the top	3.	Stretching
	4.	Splitting at sutures
	4.	Splitting at sutures
	5.	Tearing irrespective of sutures
	6.	Circumscissile tearing
Special situations	7.	Prefloral egress
	8.	Cleistogamy

fusion product of the secondary teeth and the primary traces, these being all that was left of the primary (in the sense of *Solanum*) teeth. If this were the case, could it be detected? Such a series may well have taken place in *Capsicum annuum* and other species that have calyces with reduced teeth, inconspicuous sleeves, and floral egress by stretching (Fig. 10). Thus the sequence hypothesized here, although supported only by intuition, calls for considerable caution in extrapolating evolutionary sequences to other groups. Another likelihood is that an evolutionary sequence like that outlined for *Lycianthes* has taken place in other groups and has provided the stage for evolution of structures still more advanced. Thus in the Bignoniaceae, *Amphilophium* has a well-defined sleeve not unlike that of *Lycianthes*—this should probably not be considered unique in the family, but rather an indication that other members of the family also have evolved elaborate calyx structure that cannot be readily assessed or understood on the basis of present calyces. The sleeve and secondary teeth of *Lycianthes* should probably not be regarded as unique evolutionary etudes or as phylogenetic endpoints but as stages on a larger development route travelled by many advanced plant groups.

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